The extinct macaws of the West Indies, with special reference to Cuban Macaw *Ara tricolor*

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Summary.—The best-known species of West Indian macaw, and the only one for which skin specimens exist, is Cuban Macaw *Ara tricolor*, although at least seven and sometimes as many as 15 different species of *Ara* and *Anodorhynchus* have been speculated to have formerly occurred in the Greater and Lesser Antilles. We review available historical and prehistorical evidence for the existence of these different species and conclude that only two or three, St. Croix Macaw *Ara autochthones*, *A. tricolor* and perhaps Montserrat Macaw *Ara*. sp., and can be definitively admitted, with reasonably strong evidence for another, Gosse's Macaw *Ara gossei* of Jamaica. In addition to reviewing the causes and patterns of decline in West Indian macaws, we provide a complete overview of available knowledge concerning *A. tricolor*, including details of all extant specimens (19). In particular, we draw attention to a commonly repeated error in much of the ornithological literature over the past six decades concerning the final demise of Cuban Macaw, as well as to historical data that suggest the species' range was wider than is often admitted.

Although only a few sketchy passages exist from those who saw live macaws in the West Indies, those florid descriptions give us an appreciation of the former beauty, now in large part lost, of those islands' diverse parrot fauna. Columbus described the macaws of the Antilles as 'by far the most beautiful ornaments of the gloomy forest which covered the land given up to nature' (Buffon 1774: 177). Du Tertre (1654: 294) said of West Indian macaws, 'It is the finest sight in the world to see ten or twelve Macaws in a very green tree; never are more charming colors displayed.' Gundlach (1893: 152) vividly described Cuban Macaw *Ara tricolor* as he lamented the loss of these large, long-tailed birds. Tragically, Cuban Macaw was just one of many spectacular psittacines lost in the region in historic times.

Three groups of psittacids inhabited the West Indies at the time of 'discovery' by Europeans: macaws (*Ara* and possibly *Anodorhynchus*), parrots (*Amazona*) and parakeets (*Aratinga*). Du Tertre (1667: 247) noted that 'These birds are so dissimilar according to the grounds where they procure their food, that every island has its Parrots, its Aras, and its Parroquets, different in size of body, in tone of voice, and in the tints of the plumage.' Williams & Steadman (2001) suggested that the remarkable total of as many as 60 endemic species of psittacids formerly occupied the West Indies but, as noted by Clark (1905a) and Forshaw (1978), parrots and their kin are among the first to be exterminated from any given locality, especially when confined to an insular habitat. Sadly, today only 12 species (three parakeets, nine parrots) survive in the West Indies, a loss of up to 80% of psittacid species from the region (Wiley 1991, Williams & Steadman 2001, Wiley *et al.* 2004).

The original psittacine fauna in the West Indies may have included as many as 15 species of macaws, with most Greater Antillean and several Lesser Antillean islands supporting one or more indigenous species (Williams & Steadman 2001). Although none survives today, macaws persisted into historic times on at least Cuba, Isla de Pinos, Jamaica, Guadeloupe, Dominica and Martinique, but certainly some were lost during prehistoric

human occupation of islands such as Montserrat. The fossil from the last-named island has been variously identified as a new species, an unidentified macaw, or the same species as that formerly present on Guadeloupe (see next section). Rothschild (1905, 1907a,b) concluded that the region had seven macaw species in historic times and many subsequent treatments follow his. However, it should be noted that Rothschild completely confounded much of the evidence associated with insular parrots, for example making significant errors in describing Mascarene taxa (Hume 2007; J. P Hume in litt. 2013). Most recently, Williams & Steadman (2001) listed 15 species, with evidence ranging from poor (only hearsay) to good (specimens or repeated, substantiated observations). Only four are represented by specimens: three by subfossil skeletal remains and one by entire skins and fossil partial skeletons (Walters 1995, Olson & Suárez 2008). The paucity of specimens and reliable reports has led others to tally far fewer species. Olson & Suárez (2008) found no credible evidence in support of each of the Antilles having one or two indigenous species of macaw; they noted that the archaeological record, the strongest evidence, suggested perhaps just two species in the region. Hume & Walters (2012) suggested perhaps only 3-4 species in the Antilles, noting that 'otherwise the presence of endemic macaws on other West Indian islands is extremely dubious.' Among the other 11 macaw species Williams & Steadman (2001) cited, we consider one of good reliability, one of moderate reliability and six of poor reliability; we present evidence that the three remaining macaws considered by Williams & Steadman are synonyms of other species or probably did not exist.

Aside from Cuban Macaw and the two or three species evidenced by prehistoric bones, all information is based on casual accounts by travelers, colonists and the few naturalists who resided or passed through the islands between the 15th and 19th centuries. Confounding some early reports are compilations by authors of regional or world faunas (e.g., Buffon), who cobbled together information in a way that makes identification of species and their location difficult if not impossible. Nevertheless, sufficient evidence exists to state that macaws were formerly abundant on several islands. As examples of historical abundance, Peter Martyr d'Anghera (1457–1525; *in* MacNutt 1912: 72) proclaimed that parrots and macaws were 'as numerous in all these islands [West Indies] as sparrows or other small birds are with us' [Europeans], whereas Hans Sloane (1660–1753; 1725: 297) reported 'the Small Maccaw' as 'very common in the Woods' of Jamaica, and Bryan Edwards (1743–1800; 1806: 19), who resided on Jamaica most of his life, noted that 'The parrot, and its various affinities, from the macaw to the parroquet ... are as plentiful in the larger islands of the West Indies as the rook [Corvus frugilegus] is in Europe.'

Whereas some have argued that many of the macaws described by early explorers were probably exotics, imported first by Amerindians and subsequently by European settlers, statements of du Tertre (1654: 296), repeated by Labat (1742: 212), that each island had forms distinct in plumage suggests that not all of the Antillean macaws were imported species (Hume & Walters 2012). Further, Hume & Walters (2012) noted that the observations of du Tertre and Labat on their gentle and docile nature contradicts that of mainland macaws.

Our objective here is to review the relevant historical information concerning the presence and distribution of macaws in the West Indies, and to present such scant biological information as is available. We focus on what is known of Cuban Macaw, presenting data on specimens, and examine possible reasons for the extinction of that species, as well as other Antillean forms.

Macaws in the West Indies

Unfortunately, so few data are available for most suggested species of West Indian macaw that they are considered 'hearsay species' (Greenway 1967: 315). Hume &

Walters (2012) noted that 'no other group of extinct birds has aroused such overzealous misinterpretation' as Antillean macaws. Nevertheless, much archaeological investigation remains to be done throughout the West Indies, particularly in the Lesser Antilles. Compared to many mainland areas, fossil remains are uncommon in the West Indies and little is known of vertebrate fossils, especially in the Lesser Antilles (Olson 1978, Woods 1989). Here we present additional evidence or clarify certain reports of macaws in the Antilles.

Bahama Islands.—No evidence of a macaw to date.

Cuba.—One species, Cuban Macaw, *Ara tricolor* (Bechstein, 1811), survived until the mid-19th century.

Jamaica.—At least one, perhaps three, native species, but identifications in many original accounts are muddled. Williams & Steadman (2001) thought it plausible that multiple species of *Ara* could have occurred on Jamaica, because it is a large island with diverse habitats, although it should be noted that the much larger island of Cuba, with considerably more varied habitats, apparently only ever supported one species of macaw. Nevertheless, Jamaica is one of only two of the Antilles that supports two endemic *Amazona*. Species attributed to Jamaica include Red-headed Green Macaw *Ara erythrocephala* Rothschild, 1905, Red-tailed Blue-and-yellow Macaw *A. erythrura* Rothschild, 1907, and Gosse's Macaw *A. gossei* Rothschild, 1905. Evidence is good for at least one species, although no specimen exists, but poor for the other two species. All Jamaican macaws were apparently extinct in the wild by the mid-19th century, as William T. March (1804–72; 1863), a native Jamaican and reliable observer, reported his last information on wild macaws was in 1849.

Ara erythrocephala: Greenway (1967: 320) portrayed Red-headed Green Macaw as an 'almost mythical bird,' given the tenuous circumstances upon which Rothschild (1905) established it as a unique species. Rothschild (1905, 1907a) described the bird as predominately green, with a red head, based on an account by Richard Hill (1794/5–1872; in Gosse 1847: 261–262), a resident Jamaican and trustworthy observer. More than a century earlier, Sloane (1725: 297) wrote that the 'Small Maccaw[s]'... 'are very common in the Woods, and are eaten as Pigeons, but when young, are tamed, and kept as Parrots.' Browne (1756: 472) described a 'small green long-tailed Parrot' as native to Jamaica; this was probably a small macaw, because Browne also listed both native parrots (*Amazona collaria* and *A. agilis*) and parakeet (*Aratinga nana*). But Browne does not describe a macaw similar to Rothschild's *A. erythrocephala*.

Hill (*in* Gosse 1847: 263) noted that a captive Jamaican macaw (*A. erythrocephala*?) had been purchased from hog-hunters by a Mr White of Oxford estate (Trelawny parish; *c*.18°27′00″N, 77°34′58″W; 200 m). W. Osburn (*d*. 1860; 1859) visited Trelawny specifically to search for macaws, but found none and said the local sportsmen knew nothing of it. Osburn (1859) referred to a long-term resident of Trelawny who reported 'constantly' seeing macaws but, when pressed by Osburn, recalling seeing macaws 'about four or five times in twenty-five years, ... always flying at a great height.' Osburn concluded that macaws should be listed as 'occasional wanderers' to Jamaica.

Hill (*in* Gosse 1847: 261) wrote that macaws, 'with unquestionable certainty...are occasionally, if not constantly, denizens of our mountain forests.' Further, Hill (*in* Gosse 1847: 262–263) reported macaws were found in 'the Black grounds' [Trelawny parish; 18°15′50″N, 77°31′58″W; 738 m], 'the never failing resort of these Mexican Macaws [*A. militaris*]. I have been assured that several birds have been procured there. This is said to be nearly as far eastward as they have been found.' Hill (*ibid.*) also noted that young, in 'the

first year's plumage,' had been procured in the 'neighbourhood of Accompong Maroons' (18°13′33″N, 77°45′14″W; 450 m), in the hills of St. Elizabeth parish.

Hill (*in* Gosse 1847: 261–262) thought the birds were Military Macaws *A. militaris*, which he believed migrated from the mountain ranges of the continent, where they bred, and did not return until the first part of the year. During its absence from the mainland, Hill thought it was a casual visitor in Jamaica, where the macaw inhabited the mountains. Clark (1905b) argued that it was unlikely that macaws would cross great extents of water, and thought it more plausible that such individuals represented feral birds. He agreed with Cory (1889: 178) that 'it is not impossible that *Ara militaris* may have occurred in Cuba and Jamaica, but it is improbable. The bird recorded as such was perhaps *A. tricolor* wrongly identified.' Clark (1905b) suggested that at least some species attributed to the Greater Antilles by early writers had apparently been brought from Middle or South America to Jamaica, and then were re-shipped to the Old World as native to the island.

March (1863) observed the partial remains of a macaw shot by a settler near Maroon Town (18°20′40″N 77°47′43″W; 440 m; St. James parish) in 1834. Although not a perfect match with *A. erythrocephala* as described by Rothschild (1905), March's description from memory ('the head and neck were a bright green with red in the forehead and chin, the tail blue and red, and the wing blue and green.') is closest to *A. erythrocephala* among species attributed to Jamaica by Rothschild (1907a). March's description, however, is much closer to Military Macaw than to *A. erythrocephala*.

Snyder *ct al.* (1987: 40) suggested that *A. erythrocephala* may represent Military Macaw or Great Green Macaw *A. amhiguus*, both Middle American species. Lack (1976: 255) thought the small green macaw described as *A. erythrocephala* was an endemic species derived from Military Macaw.

Ara crythrura: Rothschild (1907a) named A. crythrura based on Charles de Rochefort's (1605–83; 1658: 154) report of blue-and-yellow parrots, with all-red tails. Rothschild (1905) first named the bird Anodorhynchus coeruleus, and said it was from Jamaica, but later (1907a: 54) corrected the name to Ara erythrura nom. nov. and noted it was from 'One of the West Indian Islands.' However, Greenway (1967: 319) regarded Rothschild's description as not credible because de Rochefort had not visited Jamaica but, as others (e.g., de la Harpe 1759) and even de Rochefort noted, took much of his material from du Tertre. Greenway (1967) suggested that A. erythrura is a synonym of A. martinica [martinicus], a poorly documented form supposedly from Martinique.

Sloane's (1725: 296) 'Great Maccaw' ('Psittacus Maximus cyanocroceus') is clearly closest to Ara erythrura among those described for Jamaica by Rothschild, but Sloane's account differed: 'On each side of the Head was a redish fleshy bare Membrane near the Eyes, with some few black Feathers growing on it'; also, Sloane (1725) said the tail was blue, not red as depicted by Rothschild (1907a: Pl. 15). In fact, Sloane's bird more closely resembles Blue-and-yellow Macaw A. ararauna. Browne (1756: 472), who called it 'the blue Macaw of Edwards,' said he had observed one or two in St. Ann's (St. Ann's parish; c.18°26'25"N, 77°11′23″W), and 'yet keep some of the feathers of one that was killed there by me.' Although Browne (1756) said it was a native of Jamaica ('tho' seldom catched there'), he added that 'most of those that are generally seen about gentlemen's houses' had been 'introduced there from the main, where they are more common.' He said they were very rare in Jamaica, where they 'keep in the most unfrequented inland parts.' Coke (1808: 390) was probably referring to the same bird when he stated that 'The Blue Mackaw, a more beautiful bird, though not so gaudy as the red, is a native of Jamaica, but not common, and is wild in the woods, particularly in the parish of St. Anne.' Revd. Coward (in Gosse 1847: 261) observed macaws in flight about 1842 in 'a plain at the foot of a chain of mountains dividing [St. Elizabeth] parish from St James [parish], and consequently nearly in the medial line of the island.' Residents of the area familiar with these birds told Coward the macaws were blue and yellow, which led Gosse (1847) to assume they were *A. ararauna*. In 1836, March (1863) was told by Richard Elmas Breary, a resident of St. James, that he had seen three blue-and-yellow macaws flying high overhead on a mountain road between St. James and St. Elizabeth parishes.

Lack (1976: 253) thought the blue-and-yellow macaws were introduced, and cited the fact that no writer since March claimed *A. ararauna* (*A. erythrura*) for Jamaica. Possibly all were feral *A. ararauna*, escaped or released after transport to Jamaica as cagebirds.

Ara gossei: Of the three species suggested for Jamaica, the strongest evidence exists for Gosse's Macaw. Philip Henry Gosse (1810–88; 1847: 260), who resided there from December 1844 to July 1846, referred to it as 'Yellow-headed Macaw? *Ara tricolor'*, noting that it differed from the Cuban species and was possibly an undescribed species. Like *A. tricolor*, *A. gossei* was predominately red, but its forehead was yellow rather than red. Anthony Robinson (*ob.* 1768; *in* Gosse 1847: 260) examined a stuffed bird (now lost) shot about 1765 by a Mr Odell in the mountains of Hanover parish, *c.*10 miles east of Lucea, west of Montego Bay. Gosse (1847: 260) said it was very rare, but still it is surprising that neither Sloane (1725), who resided on Jamaica in 1687–88, or Browne (1756) recorded a macaw matching Robinson's (*in* Gosse 1847: 260) description of the bird that Rothschild (1905) would designate *A. gossei*.

Bond (1978) agreed with Lack (1976: 252–254) in rejecting the evidence that an indigenous *Ara* ('*A. gossei*') inhabited Jamaica. Wetherbee (1985) suggested that *A. gossei* was not valid, but was probably a 'tapiré' artefact; i.e., a specimen altered in its coloration by Amerindians.

In addition, non-native red-plumaged macaws were reported from Jamaica by several writers, including Browne (1756: 472), who wrote that the 'red Mackaw of Edwards ... is not a native of Jamaica, but they are frequently brought there from neighbouring parts of the Main, where they are pretty common.' Albin (1738a: 16) also reported a red-plumaged macaw ('The Maccaw from Jamaica'), considering it the male of a species in which the female was blue and yellow. A watercolour made in Jamaica by John Lindsay in 1765 depicts a probable Scarlet Macaw *A. macao* (Turvey 2010). Olson & Maíz López (2008) noted that the stylised macaw illustrated in Fisher & Warr (2003: 156) from paintings by a Lt. L. J. Robins entitled *The natural history of Jamaica* (1765) was similar to Cuban Macaw and suggested that species had been brought to Jamaica from Cuba.

Hispaniola.-Many accounts of the island's parrots have included a macaw, but its status is confused. As evidence of a macaw there, writers have referred to reports by Las Casas (1876: 298-299) and Oviedo y Valdés (1851: 443), as cited by de Armas (1888). Macaws were said to have been common formerly in Hispaniola, but rare by 1760 (Clark 1905b). Buffon (1793: 160) reported a macaw, based on the statement of resident naturalist Chevalier Lefebvre Deshayes [ob. 1786] (in litt. to Buffon 1847: 507), who stated that macaws were once very common in Hispaniola, but had become rarer and confined to tops of mountains. Olson (2005) dismissed Deshayes' statement noting it had no connection to Hispaniola. Rothschild (1905) suggested that the Ara on Hispaniola represented a species other than those already known from Cuba and Jamaica. Williams & Steadman (2001) listed it as 'Ara tricolor? or Ara unknown sp.', noting that among the three psittacids reported by Las Casas (1876: 298) on Hispaniola at the end of the 1400s was a macaw that differed from those on other islands in having a white forehead, not red like A. tricolor. Most recently, Olson (2005) examined 16th-century descriptions by Las Casas (1876) and Oviedo y Valdés (1851) and convincingly concluded that there was 'no credible evidence for the existence of a macaw on Hispaniola in historic times.' There is a record of a transatlantic shipment of 'long-tailed parrots [= macaws]' to Spain in 1494, when 60 were brought from Hispaniola to Cadiz for trading (George 1980: 80).

Based on the de Armas (1888) report, Wetherbee (1985) developed an unfounded hypothesis that Cuban and Hispaniolan macaws had been confused and extant specimens represented both species. Further, he applied the name *A. tricolor* to the Hispaniolan macaw and renamed the Cuban bird *A. cubensis*, but Walters (1995) rejected Wetherbee's revision and returned *A. tricolor* to the Cuban population, suggesting that the Hispaniolan bird probably formed a superspecies with the similar Jamaican form, *A. gossei*.

Puerto Rico.—Olson & Maíz López (2008) reported several bones of one St. Croix Macaw A. autochthones from an archaeological site in south-central Puerto Rico.

St. Croix, US Virgin Islands.—A tibiotarsus of an adult-sized immature macaw from a prehistoric archaeological site on St. Croix is the basis for St. Croix Macaw (Wetmore 1937, Olson 1978). Olson & Maíz López (2008) reported several skeletal elements from Puerto Rico. Olson (1978), Wing (1989) and Olson & Maíz López (2008), however, cautioned that A. autochthones was not necessarily indigenous to St. Croix and Puerto Rico because prehistoric West Indian people were known to trade live psittacids. On the other hand, Williams & Steadman (2001) argued that St. Croix could have sustained an indigenous macaw.

Montserrat.—An undescribed species, Montserrat Macaw Ara sp., was recently suggested to have existed on the basis of subfossil remains (University of Florida, Gainesville; UF; catalogue no. 4416) of an Ara recovered by D. R. Watters at an archaeological site at Trant's (c.16°45′N, 62°09′W), Saint Georges Parish, (Williams & Steadman 2001). However, it possibly represents 'A. guadeloupensis' (see above). As skeletons, most large parrots and macaws are sexually dimorphic in size and exhibit great individual variation (see Hume 2007) and Olson & López have suggested that the single coracoid is not diagnostic at species level and that more material is needed before any attribution can be made.

Guadeloupe.—Diego Álvarez Chanca (c.1450–1515; in de Ybarra 1907: 428) joined Columbus on his second voyage (1493–94) and reported taking 'two parrots ['Guacamayos' or macaws], very large and quite different from the parrots we had before seen' from the houses of Carib inhabitants of Guadeloupe. Two macaws have been named for the island: Guadeloupe Macaw A. guadeloupensis Clark, 1905, and Guadeloupe Violet Macaw Anodorhynchus purpurascens Rothschild, 1905.

Guadeloupe Macaw, a predominately red bird, is based on the account of du Tertre (1654: 294), who also produced a rudimentary illustration (1667: between pp. 246–247; copied by Labat 1742: between pp. 216–217). Johann Huttich (c.1480–1544; 1534: 31) recorded a red macaw 'present in such numbers as grasshoppers are with us...'. Clark (1905b) considered A. guadeloupensis as occurring on Guadeloupe, Dominica and Martinique, but later he (1908, 1934) distinguished the macaw of Dominica (A. atwoodi) from those on Guadeloupe and Martinique. Williams & Steadman (2001) found no evidence for Clark's (1905a: 269) suggestion that A. guadeloupensis also occurred on Dominica and Martinique, but concluded that it would seem more likely that the Lesser Antillean macaws were endemic to each island or set of nearby islands based on what is attributed to Jean-Baptiste Labat (1663–1738; in Clark 1905a: 269).

Hume & Walters (2012) noted the remarkable similarity between the descriptions of Guadeloupe Macaw by du Tertre (1654: 294) and Labat (1742: 212), and that this may support the presence of a macaw from the island. That similarity, however, may be the result of Labat copying du Tertre's work; several illustrations in Labat are re-renderings of du Tertre's originals. An illustration by D'Aubenton (*in* Buffon 1765–83: Pl. 12) closely resembles the descriptions of du Tertre and Labat, which Hume & Walters (2012) considered possible evidence that at least one Guadeloupe Macaw reached Europe.

Because Carib Amerindians were able to inform Columbus the direction of the mainland, Greenway (1967: 318) suggested that Guadeloupe Macaw could have been an exotic species, imported through trade with Mesoamerica or Mexico. Still, Williams & Steadman (2001) argued it was just as likely that macaws were indigenous.

Rothschild (1905) based his description of Guadeloupe Violet Macaw on Martín Fernández de Navarrete y Ximéndez de Tejada's (1765–1844; cited as 1838: ii: 425 *in* Rothschild 1907a: 55, but not found by us) account of 'le gros Perroquet de la Guadaloupe', a very large macaw of an intense purple colour', 'called Onécouli, by the Caraïbes, according to Fernand Columbus' (Rothschild 1907b: 202). Navarrete's narrative was based on Las Casas' rediscovered abstract of the log Columbus made of his second voyage, not on first-hand observations. Martyr (*in* MacNutt 1912: 72) provided more detailed and convincing evidence of a purple macaw on Guadeloupe, recounting that Columbus took 'seven parrots larger than pheasants, and totally unlike any other parrots in colour. Their entire breast and back are covered with purple plumes, and from their shoulders fall long feathers of the same colour.... The other feathers are of various colours, —green, bluish, purple, or yellow.' Greenway (1967: 320) and Snyder *et al.* (1987: 40) suggested that *Anodorhynchus purpurascens* was based on either a poor description of Guadeloupe Parrot *Amazona violacea* (now extinct) or Lear's Macaw *Anodorhynchus leari* of Brazil, which must have been imported to Guadeloupe. At best, the evidence for a Guadeloupe *Anodorhynchus* is weak.

Marie Galante.—Williams & Steadman (2001) reported a single ulna of a species referred to as 'Marie Galante (Guadeloupe?) Macaw *Ara* cf. *guadeloupensis*'; i.e., probably *A. guadeloupensis*, but an extinct species for which no specimen exists. The specimen was discovered at an archaeological site at Folle Anse (c.15°57′N, 61°20′W), Grande Anse, Marie Galante, and is deposited in the UF archeological collections (Folle Anse 68, Box 68-10). However, Olson & Maíz López (2008) examined the specimen reported by Williams & Steadman, and considered it best referred to Imperial Parrot *Amazona imperialis*.

Dominica.—Dominica Macaw *Ara atwoodi* Clark, 1908, is a poorly documented species, based mainly on Thomas Atwood's (*ob.* 1793; 1791: 29) 18th-century report of a macaw larger than native Dominican parrots (*Amazona arausiaca*, *A. imperialis*) and was 'in great plenty, as are also parrots in this island.'

Martinique.—Considerable confusion exists concerning the macaw(s) of Martinique. Williams & Steadman (2001) listed two species, 'Ara martinica' Rothschild, 1905, and 'Anodorhynchus martinicus' Rothschild, 1905, both called Martinique Macaw. In his three publications referring to extinct macaws of the West Indies, however, Rothschild does not mention two species from Martinique. Rothschild (1905) first assigned Anadorhynchus [Anodorhynchus] martinicus to a blue-and-orange macaw recorded by Père Jacques Bouton (1592–1658; 1640: 71). Rothschild used the name Anadorhynchus martinicus, nom. nov. in his paper (1907b: 202) but, in his Extinct birds (1907a: 53), he referred to it as Ara martinicus, noting Anadorhynchus martinicus Rothsch. 1905 as a synonym. We suggest only one, if any, species existed on Martinique, and propose that Ara martinicus Rothschild, 1907, be assigned to it. Certainly, whether one or two species, it is poorly documented, being based solely on Bouton's (1640) scanty account. Salvadori (1906) considered it to be Blue-and-yellow Macaw. Greenway (1967: 319) suggested Bouton described a captive bird and, with Snyder et al. (1987: 39-40), also thought that the species concerned was Blue-and-yellow Macaw, which could have been traded to Martinique. Snyder et al. (1987), however, noted that a distinctive macaw once occurred on Martinique. Regardless of its name, we agree with Williams & Steadman (2001), who suggested that both supposed species of Anodorhynchus in the Lesser Antilles require corroboration. As noted by J. P. Hume (in litt. 2013), that an Anodorhynchus macaw once occurred on the West Indies is, for now, probably best regarded as a figment of Rothschild's imagination, given that no modern-day *Anodorlnynchus* occurs anywhere near the West Indies, and all of the available evidence suggests that this genus was rare even in historical times making it unlikely that such birds would have arrived in the Antilles via trade. In contrast, several species of *Ara* macaws occur on the adjacent mainland of South and Middle America.

In 1936, the Cuban scientist Mario Sánchez y Roig (1890–1962) thought he had found a specimen of *Ara martinicus*. He claimed that it was collected in September 1845 and mounted in 1846 (*in litt*. to L. C. Sanford, 21 February 1936). On examining the specimen, however, J. T. Zimmer determined it to be a composite hoax, using the head, body and wings of Burrowing Parakeet *Cyanoliseus patagonus byroni* (now *bloxanii*) of Chile, and tail of a dove, apparently an Old World *Streptopelia*. Zimmer (*in litt*. American Museum of Natural History, 27 March 1936) noted 'It has very little resemblance to the Macaws, even in its made up condition.'

Natural history of Cuban Macaw, with comments on other West Indian macaws

Earliest records.—Columbus and others, including José de Acosta (1540–1600; 1590), Bartolomé de Las Casas (c.1484–1566; 1552–61), Diego Álvarez Chanca (1494; in de Ybarra 1907), and Gonzalo Fernández de Oviedo y Valdés (1478–1557; 1950: 167) mentioned macaws in their reports of the exploration of Cuba and other of the Antilles. Juan Ignacio de Armas (1888: 114–115) summarised these early records. Cuban Macaw's beauty was well appreciated and illustrated in early treatments based on specimens, including Levaillant (1801 Vol. 1: Pl. 5), D'Aubenton (in Buffon 1765–83: Pl. 641: 'Le petit Ara'), Bechstein (1811: Pl. 1) and Brehm (1842: Pl. 3). The court painter Leopold Brunner produced a painting of A. tricolor in the late 18th century (H.-M. Berg pers. comm.).

Relationships.—Speculation on relationships among West Indian macaw species is presently impossible because no reliable, detailed descriptions or specimens exist other than for *A. tricolor*. Williams & Steadman (2001) noted that overall the plumage of Cuban Macaw suggests that its nearest mainland relative was Scarlet Macaw, because the distribution of red and blue is similar, as is the presence of a white facial patch that is featherless except for small crescentic lines of tiny red feathers. *A. tricolor* is distinct in lacking a yellow shoulder patch, its all-black bill and substantially smaller size. Greenway (1967: 315) affirmed that *A. tricolor* was clearly a representative of *A. macao*, and believed other forms of what he considered a superspecies occurred on Jamaica, Hispaniola and Guadeloupe. *A. tricolor* and *A. macao* share a species of feather mite (see Parasites), which further supports their relationship.

Range and status of Cuban Macaw.—Early writers described the range of *A. tricolor* as not only Cuba and Isla de Pinos, but also Haiti and Jamaica (Cory 1892, Gundlach 1893, Todd 1916), but most recent authors have limited its range to the first two islands (Bond 1978, Olson 2005, AOU 2012).

Clark (1905b) stated that young *A. tricolor* was largely green, although he presented no source for this. If the juvenile of *A. tricolor* was predominantly green, that could account for early reports of *A. militaris* on Cuba and Jamaica (Clark 1905b, Williams & Steadman 2001). On the other hand, Military Macaws were imported to the islands and could have occurred in a feral state, thereby adding to the confusion (see Trade).

Cuba.—Fossil evidence exists for Ciego Montero, Cienfuegos province (22°20′0″N, 80°24′0″W; Wetmore 1928; Pleistocene); Cueva de Paredones, Caimito, La Habana province (22°84′0″N, 82°63′0″W; Arredondo 1984; Quaternary); and Casimba en Los Buentes, Mal Páez, Sagua La Grande, Villa Clara province (22°48′0″N, 80°04′0″W; Olson & Suárez 2008;

Quaternary) (Fig. 1). Arredondo (1984) said that Cuban Macaw was abundant at the time of the European arrival, although Barbour (1923: 80) suggested it probably never was widespread. Moreno (1992) considered it restricted to central and western Cuba, as well as Isla de Pinos.

The Italian Giovanni Gemelli Careri (1651-1725; Giro del mundo 1699-1700; in de la Torre 1857) mentioned killing large numbers of parrots and two macaws near La Habana on 20 January 1698. An anonymous resident ('By a physician' 1844) of Cuba listed the macaw in the 1840s, but by the mid-19th century d'Orbigny (1839) wrote that it was becoming rare. Most accounts of the macaw's range and numbers at this time are based on Gundlach's (1810-96) reports from Ciénaga de Zapata, a vast swamp comprising about one-third of the province of Matanzas, on whose southern boundary it is located. Gundlach (1893: 151) noted that the macaw was still fairly common at the swamp's northern edge (e.g., Hanábana, where the río Hanábana flows into the swamp) in 1850, but thereafter it retreated into the interior. He (1874; 1876: 126) reported it occurring from Hanábana (Hacienda Hanábana = 'Hato Zarabanda'; 22°24'0"N, 80°58'01"W; 12 m) to the Ensenada (Bahía) de Cochinos (Bay of Pigs; 22°10′48″N, 81°09′59″W; c.32 km south-west of Hanábana). Gundlach passed nine months in the Ciénaga, from September 1849 to mid 1850, mostly at its north-eastern edge (González López 1990). It was probably during his 1849-50 visit that Gundlach collected several macaws from one of the last bands, which he said came regularly to feed at Hanábana (Ramsden 1918). In early 1850, Gundlach traveled to Hato Cabeza de Toro (22°06'0"N, 80°48'0"W; 10 m; c.38 km south-east of Hacienda Hanábana, and c.39 km east-southeast of Bahía de Cochinos), but left no record of macaws in that part of the Ciénaga. Gundlach made another trip to Ciénaga de Zapata in June 1856, his first stop on an extended journey through Cuba. By 1856, Gundlach (1856) considered the macaw rare in Cuba. Barely a decade later, Gundlach (1865-66, 1873, 1874, 1876: 126) noted it was confined to only a few places, with the population consisting of a few pairs. In later years he did not find it in Ciénaga de Zapata, although Gundlach told Cory (1886, 1889: 177–178) that he believed A. tricolor still survived in Zapata about 1885.

The only report of macaws from western Cuba is that of Barbour (1923: 80), who was told of its former presence at Guane (western Pinar del Río province; 22°12′07″N, 84°05′16″W; *c*.300 km west of Bahía de Cochinos; Fig. 1); he remarked that no macaws were seen in western Pinar del Río after the great hurricane of 1844.

In 1867, Antonio Perpiña (1889), a Spanish writer, geographer and priest, traveled widely through central Cuba, some of the cayos, and as far south-east as Pico Turquino,



Figure 1. Cuba and Isla de Pinos (Isla de la Juventud) with major cities and sites mentioned in text, and known localities of Cuban Macaw *Ara tricolor* from observations (dots) and fossil specimens ('x').

Sierra Maestra (Fig. 1). Perpiña described passing through extensive virgin forests in which he found many animals, and gave a detailed and acceptable description of Cuban Macaw, which he called the 'king of the parrots' because of its brilliant colour and size. Perpiña (1889: 32) recorded that his entourage shot a macaw, six parrots, four parakeets and 23 other birds during a day of hunting in Valle de San Antonio (c.21°32'0"N, 77°28'0"W; 24 m, near Sierra de Cubitas and c.31 km east-northeast of Camagüey; Fig. 1). Later in his expedition, Perpiña (1889: 242) reported another macaw and many parrots were killed by his party near Jobabo (20°54'32"N, 77°17'06"W; 82 km south-east of Camagüey), between Guáimaro (21°03′0″N, 77°21′0″W) and Las Lomas de Rompe (Sierras de Rompe; 21°02′42″N, 77°10′55″W), west-northwest of Las Tunas (Fig. 1). Further, Perpiña (1889: 247) wrote of the great red macaw ('lorirojo') observed at Las Lomas de Rompe, where he also noted Ivorybilled Woodpecker Campephilus principalis bairdii, Cuban Parakeets Aratinga euops and other birds. Although Perpiña's observations appear credible, it is surprising that Gundlach did not encounter macaws in central Cuba, including around Camagüey in May 1859; however, Gundlach was told of macaws in central Cuba (Gundlach 1893: 151). Although Gundlach made extensive explorations of the easternmost region of Cuba, he failed to find macaws and said that no one knew of it there (Gundlach 1893: 151).

Isla de Pinos. — Gundlach explored Isla de Pinos (= Isla de la Juventud) twice, in 1854 (December) and 1855, including six weeks at Santa Fé (21°44'31"N, 82°45'18"W); he also made a five-week trip early in 1892 (Poey 1866, Gundlach 1854: 426, Dathe & González López 2002; in litt. to F. Ramsden, La Habana, 26 April 1892; JWW pers. archive). Despite these extended periods of travel, Gundlach was unable to adequately explore the extensive Ciénaga de Lanier (21°34′0″N, 82°52′0″W; 10 m) because of the distance from his base at Santa Fé (= La Fé; c.25 km north-east of Lanier) and so passed just one day at the swamp's northern edge. Although Gundlach (1893: 151) listed the macaw from Isla de Pinos, he collected none there; he was told that some macaws still survived on the edge of the Ciénaga de Lanier and reported that the macaw and Ivory-billed Woodpecker occurred in the southern Ciénaga (Dathe & González López 2002). Walter Reaves Zappey (1878–1914) traveled extensively through Isla de Pinos, collecting for Rothschild's Tring Museum in 1902, and for E. A. & Outram Bangs in 1904, but did not find maçaws. Zappey was told that the last pair of macaws known in the island was killed about 1864 at San Francisco de la Vega (21°37'0"N, 82°46'0"W; Fig. 1), 13 km north of the Ciénaga de Lanier; none was reported thereafter (Bangs & Zappey 1905, Todd 1916). The pair killed at San Francisco de la Vega apparently was not preserved (Olson & Suárez 2008). The Isla de Pinos macaws were probably subject to intense harvesting as the Cuban population dwindled. As parrots became scarcer on Cuba, harvesting became much more intense on Isla de Pinos to supply demand (Smith 1944); we suspect its macaws also became more vigorously sought for the same reason.

Because Bangs & Zappey (1905) referred to the locality of the 1864 record merely as 'La Vega,' rather than its complete name of San Francisco de la Vega, many authors (e.g., Greenway 1967, Day 1981, Luther 1995, Fuller 2001, Olson & Suárez 2008, Hume & Walters 2012) have wrongly assigned the location to La Vega, Cienfuegos province (22°05′0″N, 80°21′0″W), in Cuba, rather than to the correct Isla de Pinos location. La Vega, Cuba, is *c*.300 km east-northeast of San Francisco de la Vega, Isla de Pinos. Equally, many authors since Rothschild (1907a), especially in recent decades, have referred to this record as only having involved a single individual.

Habitat.—Cuban Macaw occupied open terrain with scattered trees, especially palm savanna, characteristic of Ciénaga de Zapata. Many years after Gundlach, Barbour (1943: 73, 1945: 152) traveled the río Hanábana to where that river flowed into the swamp, describing

the morass as bordered by a wide area of open country with scattered clumps of palms and hardwood *cayos* or hammocks. The border zone sloped gently toward the swamp and its extent varied as the rains caused the water levels to rise or fall throughout the entire Ciénaga.

Perpiña (1889) described limitless tracts of unbroken forests from north of Camagüey to Las Tunas. The natural vegetation of central Cuba was seasonal evergreen, semi-deciduous (dominated by *Swietenia mahagoni*) and gallery forests, in stark contrast to the almost complete conversion of that region to crops and pastures with only remnant forest and palm savanna today (Borhidi 1991). The habitat where Perpiña found macaws around Lomas de Rompe formerly consisted of extensive rainforest-like gallery forests, but has been impoverished by human influence, and today only a few degraded stands of forest remain; natural vegetation has been replaced by treeless marshy meadows and moist savannas (Borhidi 1991). Also, the area around Guane, Pinar del Río, is mostly converted habitat, but the flatlands and gently rolling hill country of the region originally were characterised by mixed palm-pine woodlands with a loose canopy layer, in which *Colpothrinax wrightii*, *Acoeloraphe wrightii*, *Pinus tropicalis* and *P. caribaea* were dominant (Borhidi 1991).

Ciénaga de Lanier has not been substantially altered since the mid-19th century and is today characterised by mangroves at its southern fringe, and a variety of seasonally inundated habitats including semi-deciduous forest, marshy grasslands, hardwood and palm hammocks, and palm savanna in the interior.

Buffon (1793: 161), probably speaking of more than one species of red macaw, said these birds lived in woods and wetlands with palm trees, and fed mainly on fruit of palms, of which there were immense forests in the flooded savannas. M. de le Borde (*in* Buffon 1793: 160) reported that West Indian macaws 'retire to the least frequented places, and are no more observed to approach the plantations.' Browne (1756: 472) stated that the 'blue Mackaw of Edwards' generally kept to the most unfrequented inland parts of Jamaica. Richard Hill (*in* Gosse 1847: 261) reported Jamaican macaws (*Ara* sp.) were 'found exclusively in the central mountains westward of the island, and are observed on the skirt of the partially cleared country, at an elevation of 2500 or 3000 feet [750–900 m] above the sea.' March (1863: 283) noted that all records of macaws in Jamaica were from mountainous and wooded areas, in contrast to the Cuban Macaw, which was mostly found in lowland savanna, including coastal regions, and low-elevation interior forests.

Habits.—Few data are available on behaviour of West Indian macaws, but du Tertre (1654: 294) said 'Their voice is loud and piercing, and they always cry when flying. If one imitates their cry, they stop short. They have a grave and dignified demeanor'. Labat (1742: 212) likewise noted that the voice of West Indian macaws in general was strong. Atwood (1791: 29) characterised Dominican Macaw vocalisations as a 'disagreeable, harsh noise,' and 'loud chattering noise, which at a distance resembles human voices.' Gosse (1847: 263) reported that Jamaican macaws (*Ara* sp.) flew extremely high, in pairs, giving harsh screams, before finally alighting on the 'loftiest of the forest trees, in their chosen resting places.' In Dominica, Atwood (1791: 29) said macaws gathered atop the highest trees, where they 'feed on the berries in great numbers together.' De Rochefort (1658: 154) said Lesser Antillean macaws commonly flew in flocks. Gundlach (1874, 1876) reported that Cuban Macaw lived in pairs or in families, and noted (1893) it had a loud vocalisation like the macaws of Central America.

Diet.—Gundlach (1874, 1876, 1893) characterised the diet of Cuban Macaw as including fruits, palm fruit, seeds of Chinaberry tree *Melia azedarach*, tender shoots and buds. Chinaberry tree is native to Asia, Australasia, and some Pacific islands, but has been naturalised widely in warmer parts of the world, including the West Indies. The fruit is a

slightly fleshy marble-sized (c.15 mm in diameter), nearly round drupe. The oblong seed is 3.5×1.6 mm and surrounded by pulp, which was probably the part consumed by macaws, as it is by Cuban Parrots *Amazona leucocephala* and Cuban Parakeets (pers. obs.). The fruit is mildly toxic to humans. Cuba has a diverse palm flora (Leiva Sánchez 1999) and seeds of several species that occur in Ciénaga de Zapata were probably important in the macaw's diet (Olson & Suárez 2008). Dominant species of palm there include *Roystonea regia* and *Sabal maritima*. Local palms have large fruit upon which many birds, including parrots, feed. Olson & Suárez (2008) attributed certain features of Cuban Macaw's skull to its probable diet of very hard seeds, especially those of palms, as is typical of larger mainland macaws.

In Jamaica, Browne (1756: 250) noted that the seeds of a *Sloanea* ('the large oval-leafed *Sloanea*, or brake-axe tree'; probably *S. jamaiceusis*) were 'much coveted by the mackaw and parrots,' further stating that these were the only birds that could 'break thro' those thick and lignous seed-vessels.' Further, Browne (1756: 343–344) listed two Jamaican palms—'The Mackaw Tree' and 'The Great Mackaw Tree'—but without reference to the bird. He noted that their fruits were large and rich in palm-oil. Lunan (1814: 468) said the Macaw-Tree was so called 'from a large bird that feeds upon the fruit of this tree, which is of the palm kind. There are two sorts of them...': 'great macaw-tree' and 'small macaw tree.' There may be confusion as to the true origin of the names of these palms, because the vulgar names may relate to the Portuguese name of macaúba for a kind of palm tree.

Oviedo y Valdés (1535: Libro Septimo, Capitulo ii: lxxii) reported West Indian macaws fed on manchineel *Hippomane mancinella*, which is common in the West Indies but is a powerful caustic poison to man and other animals. Du Tertre (1654: 296) said West Indian macaws fed 'on seeds and several fruits of trees, but mainly on the apples of the manchineel.' Later, du Tertre (1667: 249) elaborated, saying macaws only ate manchineel in times of necessity, and cautioned that meat of macaws that had eaten manchineel was unhealthy and even poisonous to man.

Breeding.—Unfortunately, Gundlach did not observe the breeding behaviour of *A. tricolor* as he did not visit Hanábana at the appropriate season (Gundlach 1865–66, 1873, 1874, 1876). He described the nest as a hollow in a palm based on sites shown to him by local residents (Gundlach 1876). The egg has not been preserved or described.

Atwood (1791: 29) noted that Dominican Macaws 'breed on the tops of the highest trees.' Du Tertre (1667: 249) stated 'The male and the female [West Indian macaw] are inseparable companions, and it is rare that one is seen singly', further noting, 'When they wish to breed (which they do once or twice a year) they make a hole with their beaks in the trunk of a large tree, and construct a nest with feathers from their own bodies. They lay two eggs, the size of those of a pigeon, marked like those of partridge.'

Parasites.—Du Tertre (1667: 249–250) said West Indian macaw nestlings were infested with two worms in the nostrils, with another in a small tumour on top its head, and noted that the maggots died once the chicks were feathered. These worms were probably warble fly *Philornis pici* larvae, which commonly parasitise psittacine nestlings in the West Indies (Snyder *et al.* 1987; pers. obs.). The maggots pupate within their host, and so may appear as though the larvae have died. Mey (2005) reported a new species of chewing louse *Psittacobrosus bechsteini*, now probably extinct, from a Cuban Macaw collected by Gundlach *c.*1849. Cuervo Pineda & Pérez Ortiz (2009) found a feather mite *Genoprotolichus eurycnemis* on a Cuban Macaw collected by Gundlach in 1849. This species is also known from Scarlet Macaw. Cuervo Pineda & Pérez Ortiz (2010) also found a new species of mite, *Distigmesikya extincta*, on the skin of a Cuban Macaw.

Population decline and extinction of West Indian macaws

At the time of Columbus, parrots and macaws were abundant in the islands (Huttich 1534: 31, Sloane 1725: 297, Atwood 1791: 29, Deshayes *in* Buffon 1793: 160, Edwards 1806: 19, Martyr *in* MacNutt 1912: 72), but by the 18th century macaws were rare in the Lesser Antilles (and presumably elsewhere) (Clark 1905a). M. de le Borde (*in* Brisson 1760: 183) stated 'In all these [West Indies] the Macaws have become very rare'. Seventy years earlier, John Taylor (*fl.* 1687; 2008: 142–143) noted that Jamaican macaws were 'held as a great rarity, there being but a few of them on this island and those hard to be come at, because they are noewhere to be found but in the woody mountaines.' Further observers of macaws in Jamaica also reported declining populations. Browne (1756: 472) said the 'blue mackaw of Edwards' was very rare, Stewart (1822: 79) noted that 'The maccaw is become very scarce', and Gosse (1847: 260) reported they were very rare during his residence (December 1844–July 1846). March (1863) stated that he had not heard of any reports on Jamaica since 1849, the last dependable report for the island.

Several dates have been proposed for the extinction of Cuban Macaw, including *c*.1850 (Bond 1940, Adams *et al.* 2003), *c*.1864 (Bond 1959, Balát & González 1982, Olson 2005), *c*.1884 (Vincent 1966–71, Moreno 1992), *c*.1885 (Greenway 1967, Prestwich 1970), between 1864 and 1885 (Lantermann 1984), and end of the 19th century (Garrido & García Montaña 1975, Moreno 1992). The last reliable reports, however, were Gundlach's from Ciénaga de Zapata in the early 1850s, Perpeña's in central and south-west Cuba in 1867, and possibly Zappey's second-hand record from Isla de Pinos in 1864.

Causes of extinction

Hunting.—Hunting for psittacids was a part of subsistence and traditional cultural activities of Amerindians before the arrival of Europeans. In Mexico, Hernando Cortés (Díaz del Castillo 1956) saw parrots for sale as food in the Aztec capital Tenochtitlan in 1520. Antillean Amerindians included parrots and macaws in their diets, and du Tertre (1667: 249) said that macaws were eaten regularly on some islands. The presence of macaw remains in St. Croix, Puerto Rico and Montserrat kitchen middens supports this. On Dominica, Columbus' men were shocked to find 'popingiayes' (macaws) along with geese, ducks and human flesh in earthen vessels, presumably being food larders, in houses of natives (Huttich 1534: 31, Arber 1885: 30).

West Indian macaws were easily killed, even using bow and arrows (Labat 1742: 81). Martyr noted the ease at which macaws could be captured by hand or noose, and the curious fact that they were not alarmed by gunshots (*in* Buffon 1793: 162, MacNutt 1912: 409). Du Tertre (1654: 294) said West Indian macaws were 'far from being alarmed by many shots fired under a tree where they are perched, they gaze at their companions who fall dead to the ground without being disturbed at all, so that one may fire five or six times into the same tree without their appearing to be frightened.' de Rochefort (1658: 154) considered Lesser Antillean macaws 'bold and resolute, for they are not alarmed by the report of firearms, and if none are wounded at the first discharge, they await a second without moving from the place where they are; but there are many who attribute this boldness to their natural stupidity rather than to their courage.'

Du Tertre (1667: 248–249) described how Amerindians in the Antilles captured macaws alive. The hunters waited until they descended to the ground to feed on fallen fruit, at which point the men stealthily approached, surrounding the birds, then burst forth, shouting and clapping, which startled the birds so that they did not fly, but fell on their backs and defended themselves with bills and claws. The Indians shoved sticks at the birds,

which they grasped with claws and beak, whereupon the birds were tied up with vines. In Cuba captive parrots were used as decoys. A native equipped with a captive parrot and a noose would climb a tree, where he hid in a straw 'hide.' When the trapper touched the decoy parrot's head, it cried out and attracted other parrots. The noose was slipped over the head of any inquisitive parrots, its neck wrung and let fall to the ground (Krieger 1929: 44).

Live macaws and parrots were kept captive until such time as they became meals for Amerindians. Huttich (1534: 31), speaking of *Ara guadeloupeusis*, noted 'they feed some of them so that they are better to eat.' Martyr (*in* MacNutt 1912: 72) reported that macaws and parrots were kept in captivity by Amerindians, 'and just as we keep magpies, thrushes, and similar birds to fatten them, so do these islanders also keep birds to eat, though their forests are full of parrots.'

Parrots, including macaws, were hunted as food by 15th and 16th-century explorers (Cooper & Armitage 2013), though they were probably eaten by the Europeans far less than by native peoples, and then only in desperation (Boehrer 2004, Cooper & Armitage 2013). Still, Labat (1742: 215) noted that while in Guadeloupe he ate more parrots than partridges when in Europe. Long (1774: 865, 951) noted that parrots were eaten by Amerindians but, although he listed parrots and parakeets, he did not include macaws among birds commonly eaten by Jamaican colonists. The reason for macaws not being eaten by Europeans may relate to the quality of their flesh. Du Tertre (1654: 294) said of West Indian macaws, 'The flesh of this bird is very tough, and considered by many unwholesome, and even poisonous.' Atwood (1791: 29-30) described the flesh of the Dominican Macaw as '...being very fat, it wastes in roasting, and eats dry and insipid; for which reason, they are chiefly used to make soup of, which is accounted very nutritive.' Conversely, Taylor (2008: 142–143) noted that the flesh of Jamaican macaw (Ara sp.) was 'very good but they are seldom eaten.' Sloane (1725: 297) said 'the Small Maccaw' was 'eaten as Pigeons', and further noted that other native parrots were eaten, including the 'common parrot of Jamaica' (Yellow-billed Parrot Amazona collaria) which he recorded as being 'bak'd in Pyes' and tasting of pigeon. This is more or less seconded by Coke (1808: 391), who stated that 'There are two species of parrots in the woods, natives of the island, both green; but one sort has a yellow bill. They are neither so beautiful, nor such good talkers, as the gray and green of other countries; they are, however, esteemed as delicate food, and are served up at some tables in preference to pigeons.' Browne (1756: 473) noted that parrots were 'generally reckoned very delicate meat, and eat not unlike pigeons; ... and frequently served up at gentlemen's tables in all the country parts of the island [Jamaica].' M. de le Borde (in Brisson 1760: 183) stated 'In all these [West Indies] ... the inhabitants destroy [macaws] for food.' The price commanded by parrots as game is suggested by Taylor (2008: 142), who wrote that 'you may bie of them dead for two royalls a duzen... at Jamaica.'

Several writers have pointed to hunting as contributing to Cuban Macaw's extinction (Rothschild *in* Lönnberg 1928, Barbour 1943, Arredondo 1984). Greenway (1967) noted that hunting was the only known reason for its extinction. Apparently, as reported for other West Indian macaws, Cuban Macaws were easily taken; Barbour (1943) was told that adults were stupid and slow to take flight when approached. Gemelli Careri (1699; *in* Pérez de la Riva & Berthe 1971) commented on the tasty flesh of Cuban Parrots, but diplomatically remarked that the Cuban Macaw should be conserved for the beauty of its feathers. Gundlach (1865–66, 1873, 1874, 1876) was more direct and noted that macaw flesh was undesirable, being tough and having an especially unpleasant odour (Gundlach 1893). Nevertheless, it was killed for food (Greenway 1967) and Todd (1916) noted it was even valued for its meat.

Trade.—Harvesting activities began even before the European arrival, with substantial numbers of animals (including macaws) captured by Amerindians for pets or trade among islands (Olson 1982, Wing 1989). Olson & Maíz López (2008) suggested that some populations of West Indian macaws may have been so precious in trade that every possible nest was sought to obtain young birds, and that vigorous harvesting of such large and comparatively uncommon species might conceivably reduce populations to extinction over the nearly 2,000 years that some islands had been occupied. They further suggested that Amerindians may have maintained the last Hispaniolan macaws in captivity, even after their extinction in the wild but, with the collapse of their cultures soon after the European arrival (Rouse 1992), the macaws became extinct.

The earliest explorers' accounts strongly suggest macaws were kept commonly as pets and perhaps bred in captivity by Amerindians (Greenway 1967, Dunn & Kelley 1989). Although adults were taken alive, nestlings were preferred as companion birds, but du Tertre (1667: 249) noted that adults could be tamed even when caught by such traumatic methods as described above. In northern Mexico and the American south-west, where they do not occur naturally, macaws (mainly Ara macao) were an important item of commerce and ritual among Amerindians, and large captive-breeding facilities were used to sustain ritual sacrifices (Hargrave 1970, Minnis et al. 1993, Creel & McKusick 1994). Bernal Díaz del Castillo (1492-1584; 1956: 212) described Hernando Cortés' entrance into Mexico City, where he found a royal zoo containing birds of all sorts, including 'parrots of many different colours, and ... so many of them that I forget their names.' Cortés (in Boehrer 2004: 56) described the Aztec zoo as superior to any in Spain. Smith (1937) noted that Columbus was 'astonished at the swarms of tame birds at liberty in the villages' of Cuban Amerindians. Chanca (in de Ybarra 1907) reported Columbus' men took two macaws from the houses of Caribs on Guadeloupe in November 1493. Being the largest and most colourful of West Indian parrots, macaws were probably of great prestige and value, and would have been traded afar.

In addition to native species, Amerindians may have imported macaws from the mainland. The husbandry and trade in live psittacines by West Indian people has raised concern among archaeologists and biogeographers who analyse material excavated from cultural sites (Wing 1989, Williams & Steadman 2001). Prehistoric peoples transported animals for trade and sustenance on their passages among islands, thereby confounding the determination of the former number and original distribution of macaws and other psittacids (Oviedo 1959, Wilson 1990, Williams & Steadman 2001). Thevet (1971) reported that native peoples carried macaws with them during war against enemies, '...for to eate them, and other things.' Olson (1982) presented evidence of bird transportation and extinctions caused by early man, noting that a lively trade in macaws existed between Indians in tropical Mexico and those in south-west North America, and suggested that trade in macaws probably also occurred in the West Indies.

Besides using macaws and other psittacines as barter and as pets, they were vigorously sought by Amerindians for their feathers, to decorate ceremonial dress and otherwise enhance the body (Labat 1742: 85, Navarrete 1828: 277, 280, Krieger 1929). An account of Francisco de Orellana's 1542 exploration of the Amazon describes local Indians keeping macaws as a source of ceremonial feathers (Heaton 1934: 415). The value native people placed on parrot feathers was recorded by Amerigo Vespucci who noted that those peoples' riches consisted in part 'of variegated birds' feathers,' and one tribe presented him with 'feathers of very great value, ... and ... numberless parrots of different colors' (Waldseemüller 1907: 98, 109). Du Tertre (1654: 294) noted that 'The natives [of Guadeloupe] hold the feathers of the tail [of macaws] in great esteem; they stick them in their hair, and pass them through the

lobe of the ear and the septum of the nose to serve as mustaches, and consider themselves then much more genteel and worthy of admiration of Europeans.'

Macaws and parrots were among the valued items traded by Amerindians for the trinkets brought to the Antilles by the earliest European explorers and, in turn, were displayed among the treasures as those explorers returned to Europe. Columbus traded red caps, bells and glass beads to natives, who in turn gave him such things as they valued most, including gold and parrots (Navarrete 1828: 42, 45, 186, Dunn & Kelley 1989: 65, 71, 223, 259, 271). In fact, Columbus was eager to obtain macaws and requested these from Amerindians who readily supplied them (Navarrete 1828: 186). In Columbus' triumphant march to Barcelona, he paraded his most cherished and representative treasures, leading his entourage on horses and mules, with captive Indians adorned with feathers and various bright ornamental apparel, their ears decorated with gold pendants, their arms with bracelets and wearing bead necklaces. Red-and-green parrots perched on their shoulders. All of these treasures Columbus presented to the king and queen (Collis 1977: 108, Davidson 1997: 285). Oviedo y Valdés (1535: Libro Segundo, Capitulo vii: ix) recorded that Columbus arrived in Barcelona with riches including gold, native Indians and many macaws. Martyr (in MacNutt 1912: 65) related that Columbus returned from his first voyage with 'some forty parrots, some green, others yellow, and some having vermilion collars like the parrakeets of India...; and all of them have the most brilliant plumage. Their wings are green or yellow, but mixed with bluish or purple feathers, presenting a variety which enchants the eye.' Morison (1970: 435) recounted that Antonio de Torres, returning from Hispaniola to Cadiz, in March 1494, brought 'sixty parrots of different colors, eight of them being big as falcons and the fairest species of fowl that fly in the air.'

Throughout the Age of Exploration of the New World, travelers brought specimens of exotic animals to Europe: live, to be exhibited in royal collections, dead, for museum cabinets (George 1980). As travel to the New World increased with accelerating exploration and colonisation, so did trade. Much as did the Amerindians, Europeans valued macaws and carried them among islands and to the mainland from the beginning of commerce in the New World. The Italian naturalist, Ulisse Aldrovandi (1522–1605) saw his first macaw at Mantua, Italy in 1572, and remarked that they were then of great admiration and were highly esteemed, and that the nobility gave them to one another as rare and valuable presents (in Buffon 1793: 157). Although parrots were considered novelties during this era, before long the entrepreneurial nature of adventurers and travelers recognised the trade value of parrots in the Old World. In fact, so many were brought back to Europe that a mere 34 years after Columbus' first voyage, Oviedo y Valdés (1950: 167) wrote 'there are many parrots, and of so many kinds and diversity, that it would take a long time to describe them, but because so many are brout to Spain, I will not waste time talking of them.' Similarly, Labat (1742: 211) stated that West Indian psittacines were too well known for him to waste time portraying them. Long (1774: 896), writing for a European audience, said of Jamaica's five species of psittacines, including 'Blue Mackaw', 'These are all native, and too generally known to need any description.' Nicolaus Joseph Freiherr von Jacquin's (1727-1817) expeditions to the Caribbean islands and elsewhere in the New World, 1754-59, resulted in large collections of natural history objects, but Jacquin (1784) did not include Ara tricolor among those species reported from his exploration of Cuba (1759) and, in fact, he was given instructions by Emperor Francis I not to collect parrots (C. Riedl-Dorn pers. comm.), again, probably because these birds were already so well known in Europe.

As Europeans rapidly became familiar with New World parrots, their desire to own these exotic status symbols continued to increase. The number of species described from captive birds attests to the multitude of psittacine species and numbers that were kept as pets in Europe in the 17th and 18th centuries, particularly among the upper classes and especially the nobility (e.g., Albin 1738a, 1740, Edwards 1751). Edwards (1751: Pl. 161) stated that 'the large Green Parrots, [are] commonly brought to us from the West-Indies,' and elsewhere (1751: Pl. 161) said the 'Great Green Parrot, from the West-Indies' was 'pretty common in London.' Edwards (1751: Pl. 168), speaking of the 'Little Green Parrot,' said '...I take it to be from the West-Indies, from whence most of the Green Parrots we have in London are brought.' Further, authors of descriptive works on parrots frequently mentioned several London and European dealers specialising in foreign birds, including macaws. Apparently even stuffed parrots found a market in Europe, as Edwards (1751: Pl. 173) mentioned buying a 'beautiful and rare little Parrot ... exposed to Sale (stuffed, and set on a Perch) in a Toy-Shop Window, in London'.

The great incentive to harvest parrots for European trade can be appreciated from the high prices commanded by macaws and others of their tribe there. Even in their native islands, psittacines were worth a considerable sum of money. For example, of Amazona parrots, Taylor (2008) recorded that '...a young one alive out of the nest will cost six royalls [reales] at Jamaica.' But captive parrots were valued far more in Europe. As examples, Albin (1738b: Pl. 13) wrote that a 'Laurey from the Brasils' [Purple-naped Lory Lorius domicella] sold for 'twenty Guineas,' the equivalent in today's money of c.£1725; Blue-and-yellow Macaw was 'commonly sold for ten Guineas' (c.£860 today) (Albin 1840: Pl. 10); and the 'Maccaw from Jamaica' [likely Ara gossei, but perhaps A. macao], which was 'commonly brought from Jamaica, and other parts of the West-Indies,' were 'commonly sold for ten Guineas' (Albin 1738a: Pl. 16). About 1680, the cost of a parrot in Amsterdam was recorded as 'roughly sixty guilders' (Margóesy 2010), when a guilder was a 10.61 g, 90% pure silver coin, demonstrating the high value of pet birds. Such prices initially made owning a macaw or parrot accessible only to the affluent and thus a substantial status symbol in Europe. But as more parrots were imported, classes other than the nobility and aristocrats were able to acquire them. Thus wealthy merchants and affluent citizens sought the parrots that were becoming staples in the growing number of bird dealers' shops. Thomas (1983) wrote that commercial bird dealers first appeared in England 'in Tudor times and in the late seventeenth century there was a large London market in singing-birds, some caught at home by professional bird-catchers, others exotics imported from the tropics.' Trade in parrots continued to increase into the 19th century, with parrot popularity as household animals reaching its peak in the 1800s (Boehrer (2004). This high point in the importation of psittacines coincides with what is probably the period when the last West Indian macaws became extinct.

Macaws were kept as companions by colonists in the islands. Du Tertre (1667) included an illustration depicting what appears to be a macaw perched at a 17th-century plantation. Taylor (2008) noted that macaws were 'kept tame as a curiosity' in Jamaica, and Gosse (1847: 263) reported that a captive Jamaican macaw kept by a Mr White was 'for some time the admiration and talk of the country round.'

Trade in all Cuban psittacines has long been a cause of concern (Gundlach 1893, Bangs & Zappey 1905, Todd 1916, Noegel 1979) and is vigorous today, even under national and international regulation, bringing about modern declines. The enormity of the trade in recent times is particularly well documented on Isla de Pinos, where parrots and parakeets were formerly numerous (Gundlach 1893, González Alonso *et al.* 2012). Gundlach (1893) predicted that if rates of capture for the pet trade were maintained, the parakeet would be exterminated on Isla de Pinos in a few years. Sadly, his prediction was fulfilled; the parakeet was extirpated early in the 20th century (Bangs & Zappey 1905). The parrot, however, has survived there, albeit in much-reduced numbers.

Although we have found no data to appreciate how many macaws and other psittacids were being exported during the 16th through 19th centuries, the few statistics of the enormous parrot trade in Cuba during the early 20th century provide an appreciation of the international demand in that period. During the first decade of the 20th century, some 3,000–5,000 pairs of parrots were exported from Isla de Pinos to the USA annually (Anon. 1910a). Because of their depredation of crops, parrots were unprotected until 1909. Numbers increased rapidly thereafter, but protests by planters soon led to the protective legislation being repealed and within a few years large numbers were again being exported; e.g., one large shipment of 2,500 parrots in 1910 (Anon. 1910b,c) and *c*.1,000 birds imported by one US dealer in July 1914 (Anon. 1914). It is certainly within reason to assume that the Cuban Macaw was even more desirable than parrots and parakeets (Olson 1982).

Cuban Macaws were kept locally and also exported to private collectors and royal and public zoos overseas, leading several writers to suggest that harvest for the pet and commercial trade was in large part responsible for its extinction (Gundlach 1874, Lönnberg 1928, Moreno 1992, Dathe & González López 2002). Local interest in Cuban Macaws as pets had a long and consistent history, until the time of its extinction. Gundlach (1865–66, 1873, 1874, 1876) reported that the macaw was a much sought-after cagebird, but noted (1874) that captives damaged furniture and other items using their powerful bills. Yet, despite this, we suspect that the macaw was a more desirable pet in Cuba than Cuban Parrot, which continues to be vigorously sought by island residents and, despite strong legal protection, is common in households.

Cuban Macaws were equally popular overseas. García Montaña (1980) said that they were given to the kings of Spain, and that over the centuries thousands were exported to Europe. Barbour (1943) supported that claim and Finsch (1863) stated that it was well known in captivity in Europe, but even so was rare. Lönnberg (1928) suggested that at one time Cuban Macaw had been very popular and that it was kept as an ornamental bird in Sweden in the 1700s.

The ever-increasing local and international demand for parrots certainly had a devastating effect. Lönnberg (1928) recognised the problem of such harvesting of young macaws in that natural reproduction was greatly reduced. As populations of native macaws diminished and it became more difficult to supply local demand, exotic species were imported to meet it. Exotics from other islands and beyond were imported to supply cagebirds for local markets in the face of dwindling native populations. Importing macaws and parrots during the colonial period is particularly well recorded in Jamaica, where, as early as the 17th century, Taylor (2008) wrote that the 'Affrican or Guinea parrat' (Grey Parrot Psittacus erithacus) was 'brought to Jamaica and sold at reassonable rates.' Regarding Grey Parrot, Edwards (1751: Pl. 163) wrote 'I am well assured that what we have are brought from Africa, generally by the Way of the West-Indies, by our Guinea Traders, that supply our Sugar Islands with Negroes.' Sloane (1725: 297) also reported that Grey Parrot was 'brought to the Island of Jamaica in great Quantities from Guinea' [Africa]. Further, Sloane (1725) said 'Psittacus viridis alarum costa superna rubente' [Red-shouldered Macaw Diopsittaca nobilis or Yellow-crowned Parrot Amazona ochrocephala; neither from the West Indies] was brought to Jamaica 'from the Spanish Main, or Continent of America frequently hither'. He also noted that Cuban Parrots were 'brought from Cuba to Jamaica frequently.' In addition, Sloane (1725: 296) recorded that 'the Great Maccaw' 'Psittacus Maximus cyanocroceus' (Ara ararauna of South America) was kept in captivity. Browne (1756: 472) noted that most of the 'blue Mackaw[s] of Edwards' were introduced to Jamaica from the mainland. Further, Browne (1756: 472) said the non-native 'red Mackaw of Edwards Psittacus maximus Jons' was frequently brought to Jamaica from the neighboring parts of the main'.

Further evidence of extensive trade in exotic macaws in Jamaica comes from a painting by the Revd. John Lindsay dated 1765 and part of a series of volumes of watercolour illustrations and manuscript descriptions of Jamaican flora and fauna in the collection of the Bristol City Museum and Art Gallery. The macaw appears to be Scarlet Macaw, and probably represents a captive individual or introduced population (Crane 1981, Fisher & Warr 2003, Turvey 2010). Scarlet Macaw was one of the most popular of parrots among 18th-century Parisian nobility (Robbins 2002) and was widely traded in the Americas by pre-Columbian Amerindians (Olson & Maíz López 2008). Thus, the species could have been imported to Jamaica via trade.

One of the attractions of psittacines as pets is their ability to 'speak', and that capacity was often noted by early writers. Taylor (2008) reported that Jamaican macaws 'spake much plainer and lowder than any parrat whatsoever.' Labat (1742: 212) noted that West Indian macaws could be tamed and, especially if taken young, spoke very well, their voices being strong and distinct. Sloane (1725: 296) said a Jamaican macaw, probably *A. erythrura*, was 'more Articulate than any Bird I ever heard.' In contrast, accounts gave Cuban Macaw poor marks regarding speaking ability. Gemelli Careri (*in* de la Torre 1857) remarked that Cuban Macaws could not speak. Gundlach (1865–66, 1873, 1874, 1876) said that although it imitated some words, Cuban Macaw did not have the skills of Cuban Parrot. It is probable, however, that ability to talk took second place to the size and showiness of macaws. Several other observers noted their poor speaking abilities. Of Lesser Antillean macaws, de Rochefort (1658: 154) commented that the tongue was 'too thick to enable them to speak as well as parrots and the smaller parakeets', and Atwood (1791: 29) said macaws 'cannot be taught to articulate words.'

West Indian macaws were often kept in royal menageries and public zoos. Taylor (2008) said that he saw one Jamaican macaw ('marcough' *Ara* sp.) 'amongst His Majesty's birds at Saint James's Park [London].' Moreno (1992) noted that many Cuban Macaws were exported to Europe where they were sought for exhibit in zoological gardens. Cuban Macaw was probably not rare in zoological collections in Europe judging from the number of specimens preserved after dying in zoos. In total, six specimens are known to have been kept previously in zoos, while an additional four were probably held as captives (Table 1). Additional Cuban Macaws were also reported in zoos, but are not known to have been deposited in museums after death; e.g., Bolle (1856) reported one in the London Zoo on 2 January 1856 (perhaps BMNH 1858.5.13.1?).

Habitat destruction.—D'Orbigny (1839: 120–121) noted that Cuban Macaw was becoming increasingly rare as natural lands were cultivated in association with human population growth. Later writers also considered habitat destruction as probably contributing to the macaw's extinction (e.g., García Montaña 1980, Moreno 1992, Dathe & González López 2002). Of particular harm was the way in which nestlings were obtained for trade. Gundlach (1893) described how adults were observed to find the nest tree, then the harvester would wait until the chicks were well grown before felling the tree to obtain the nestlings. Some chicks undoubtedly died as a result, but a more serious and long-lasting effect was the cumulative loss of the best nesting habitat; i.e., palms with cavities of sufficient dimensions and security. After many years of such selective destruction, macaws may have been left with few, and possibly only suboptimal, nest sites. This method of harvesting psittacine chicks in Cuba has continued to the present, to the point that such habitat destruction has greatly affected populations of the two surviving species (de las Pozas & González Alonso 1984, Kirkconnell & Wiley in prep.).

This practice was also common on other islands and may have affected their macaws as well. Taylor (2008) wrote that parrots and parakeets in Jamaica 'commonly breed in the

TABLE 1

Museum specimens of Cuban Macaw *Ara tricolor* known or suspected to have originated as zoo captives or cagebirds.

Museum ¹ and catalogue no.	Zoological institution where formerly held	Comments
BMNH 1858.5.13.1	Presumably a captive bird	Obtained from the Zoological Society (Knox & Walters 1994).
WML D645	Knowsley Park aviaries of 13th Earl of Derby	Died March 1846; arrived in museum 1851.
MNHN 2000-725	Jardin de Plantes, Paris	Donated to museum in 1842 after its death (Jouanin 1962).
NMW 50.796	lmperial Menagerie, Schönbrunn	Died 1835 (Fitzinger 1853) or ≥ 1806 (Moreno 1992).
SMNG A03466a	?	Probably a cagebird (C. Dücker pers. comm.).
NRM 569592	?	Thought to have been a cagebird in Stockholm; wing feathers clipped (U. Johansson pers. comm.).
NRM 523094	Amsterdam Zoo	Died 1858
SMTD 3466	?	Probably formerly a captive, by its frayed plumage (M. Päckert pers. comm.).
MCZ 72526	?	Obtained from Lafresneye Collection, France; with one clipped wing,
AMNH 205178	Zoological garden of Berlin	Presented to museum by Barbour, 1923.

¹Abbreviations: BMNH = Natural History Museum, Tring; WML = World Museum, Liverpool; MNHN = Muséum National d'Histoire Naturelle, Paris; NMW = Naturhistorisches Museum, Wien; SMNG = Senckenberg Museum für Naturkunde, Görlitz; NRM = Naturhistoriska Riksmuseet, Stockholm; SMTD = Staatliches Museum für Tierkunde, Dresden; MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts; AMNH = American Museum of Natural History, New York.

hollow trunck of cabadge trees up in the mountains soe that they are hard to come by, and you must fell the tree to come at 'em.'

Crop pest.—Gundlach (1865–66, 1873) mentioned that Cuban Macaws may have caused damage to fruit trees, but noted (1874, 1876) that, because they lived far from dwellings, the damage was not great (but added, also, that the bird provided no benefit). Hill (in Gosse 1847: 261) noted that macaws in Jamaica fed in 'small companies' on the 'full-eared maize, while the grain was soft, milky, and sweet, and the very husk was sugary.' There is no reason not to believe that Cuban Macaw also depredated crops and, as a consequence, was persecuted. Today, Cuban Parrots and, especially, Cuban Parakeets are soundly punished for such infractions!

Hurricanes.—Barbour (1923) reported that Cuban Macaw disappeared from western Pinar del Río after the great hurricane of 1844 (4–5 October). Even if that storm did not eliminate the last macaws in western Cuba, the devastating hurricanes of 1846 (the 'Great Havana Hurricane'; 10 October; Category 5) and 1856 (late August; Category 3) could have further decimated remnant and fragmented habitat, and scattered populations beyond recovery. Similarly, a strong tropical storm ravaged Ciénaga de Zapata on 21 August 1851. When original forests are extensive, hurricanes have positive effects, producing habitat for cavity-nesting birds. However, once macaw populations were restricted to a few, relatively small areas of fragmented habitat, a direct hit by a powerful storm could destroy sufficient critical habitat to cause extirpation (Wiley & Wunderle 1993). Some of the small, disjunct populations of the Critically Endangered Puerto Rican Parrot Amazona vittata were probably destroyed by such events (Snyder et al. 1987). Not only did those populations suffer the

direct effects of the storm, but habitat critical to their survival was severely damaged. Further, in the aftermath of hurricanes, parrots were more vulnerable as they moved to hostile areas seeking food, meeting humans also desperately seeking to survive.

Disease.—Imported pets and domestic fowl may have carried exotic diseases, which could have spread to wild indigenous parrots, and against which they had little or no resistance. Du Tertre (1654: 294) mentioned that although Guadeloupe Macaw was long-lived ('live longer than a man'), they were 'almost all subject to a falling sickness [epilepsy].' Labat (1724: 217) also remarked on the long-lived psittacids of the West Indies, and their susceptibility to the 'falling sickness.' De Rochefort (1658: 154) noted that Lesser Antillean macaws were 'so sensitive to cold that it is difficult to bring them across the sea.' Williams & Steadman (2001) suggested that a disease outbreak, combined with hunting pressure, caused the extinction of Guadeloupe Macaw.

Specimens of Ara tricolor

No modern skeletal specimens of *A. tricolor* exist (Williams & Steadman 2001) but we can account for 19 skins or mounted specimens in 15 collections (Table 2). All were collected in Cuba, or from an unknown locality. When and from where and whom the museums obtained these specimens is unresolved in many cases.

Gundlach's specimens.-Gundlach collected several of the last group of Cuban Macaws that came regularly to feed at a site in Ciénaga de Zapata in 1849-50 (Barbour 1923). These may have been the only macaws Gundlach collected, because he does not mention additional specimens taken during later visits to the Ciénaga. If true, Gundlach must have kept several specimens for years, eventually giving all but one to friends and institutions. Before he left Germany for Cuba in November 1838, an organisation was formed to furnish support funds by the sale of stock, to be repaid by Gundlach with specimens collected during the expedition, which was originally planned to continue to Surinam. Although Gundlach made it only as far as Cuba, he set to work collecting and shipping materials to those who had bought stock, not ceasing until he paid all his debts. Even after meeting his financial obligations, he continued to send specimens to Germany, including his precious macaws.

Cory (1889) mentioned that Gundlach had several macaw specimens, by which time Gundlach had dispersed a good portion of his collection to foreign institutions. Although Gundlach did not record how many macaws he collected, it was at least four (see below). By the time of his death in 1896, only one remained at the Instituto de Segunda Enseñanza, where Gundlach's collection was maintained (Ragués 1914).

During the mid-19th century, it became fashionable among wealthy Cubans to adorn their drawing-rooms with natural history specimens, and Gundlach gifted friends and

TABLE 2
Distribution of known skin or mounted specimens of Cuban Macaw *Ara tricolor* among 15 collections worldwide.

Collection	No.
IES	1^1
BMNH	2
WML	1
MNHN	2
NMW	1
ZMB	1
SMF	1
SMNG	1
NRM	2
SMTD	1
EHM	1
RMNH	1
MCZ	1
AMNH	1
USNM	2
Σ	19

¹Stolen in 2007.

acquaintances specimens he had prepared. He thus became known to the most influential citizens of that day, who in turn provided him with assistance (Ramsden 1918). Gundlach may have included one or more macaw specimens among those given to Cuban friends and patrons (see below).

Specimens in Cuban and foreign institutions

Instituto de Ecología y Sistemática (IES), La Habana, Cuba One: CZACC-6.59937. No date or precise locality; coll. Juan Gundlach. Adult. Mount. Specimen no. 165 from the Gundlach collection formerly in the Instituto de Segunda Enseñanza, it was stolen from IES in 2007.

Natural History Museum, Tring (BMNH) Two: BMNH 1851.7.21.5. No date (received no later than 1859), locality or collector. Adult. Skin, ex-mount. Purchased from Lt. A. Smith, but R. Prŷs-Jones (pers. comm.) thinks this may be in error, and all that can be said safely is that it was purchased. Knox & Walters (1994) noted that the correct registration number should be 1851.7.24.5. BMNH 1858.5.13.1 No date, locality or collector. Adult. Skin, ex-mount. Source given as Zoological Society and presumed to have been a captive bird (Knox & Walters 1994).

World Museum, Liverpool (WML) One: D645. No date or collector. Locality given as 'Mexico'. ♀. Skin. Obtained from Knowsley Park aviaries of 13th Earl of Derby, where it died March 1846. Acquired in 1851, and maintained today in Derby Collection.

Muséum National d'Histoire Naturelle, Paris (MNHN) Two: MNHN 2000-725. No date, locality or collector. Adult. Mount. Maintained in captivity in Jardin de Plantes, Paris, from 30 May 1840 and, after its death, on 6 October 1842, presented to MNHN by L. F. E. Rousseau (1788–1868), an assistant naturalist at MNHN (1834–60) (from *Catalogue des Animaux morts à la ménagerie 1840–1853*, where noted 11 October 1842; A. Previato pers. comm.). MNHN CG 2000-726. No date, locality or collector. Adult. Mount. Type. Jouanin (1962) noted it as from 18th century. M. Portas (pers. comm.) believes it was from old collection of Jardin du roi (museum before Revolution = pre-1789). It formed part of the 'Exposition permanente des Produits de l'Algérie et des Colonies,' displayed in the Palais del'Industrie in Paris in 1860, and curated by Aubry-Lecomte, but no information as to duration of exhibit or when transferred to MNHN (A. Previato pers. comm.).

Naturhistorisches Museum, Wien (NMW) One: NMW 50.796. No date, locality or collector. ♀. Mount. Obtained from Imperial Menagerie of Emperor Franz II (Franz I of Austria; 1768–1835) (de Germiny 1937; G. Heindl pers. comm., H.-M. Berg pers. comm.). Acquired by NMW in 1832, the same year it died at the menagerie (Fitzinger 1853: 166; H.-M. Berg pers. comm.), although Moreno (1992) set date of acquisition as 1806. Fitzinger (1853: 86) listed two *A. tricolor*, a male and female, in the menagerie as from 'Brasilien. 1760,' but G. Heindl (pers. comm.) noted that one of these birds was probably *A. macao*. G. Heindl (pers. comm.) suggested the two specimens, including the Cuban Macaw, from 1760 were collected during Nicolas Joseph Jacquin's expeditions to the Caribbean islands in 1754–59, including Cuba in 1759, but Jacquin (1784) does not include *A. tricolor* among species reported by his expedition (C. Riedl-Dorn pers. comm.).

Museum für Naturkunde, Zentralinstitut der Humboldt-Universität, Berlin (ZMB) One: ZMB 24886. No date or locality; coll. Gundlach, probably in 1849 [1850?] at Hanábana, Ciénaga de Zapata (Stresemann 1954). 3. Adult. Skin. Sent by Gundlach to ZMB in November 1880 (letter from Gundlach to Peters, 16 November 1880; S. Frahnert pers. comm.). Received by ZMB in December 1880.

Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (SMF) One: SMF 17345. No date, locality or collector. Ex-mount. From Hartert Coll. (No. 2399) (Mertens & Steinbacher 1955).

Senckenberg Museum für Naturkunde, Görlitz (SMNG) One: SMNG A03466a. No date, locality or collector. & Mount. Possibly a cagebird (C. Düeker pers. comm.). Donated (without year) to 'Naturforschende Gesellschaft zu Görlitz' by Dr H. Böttcher (1834–1904)

from village of Quolsdorf. Böttcher bought the macaw from G. Schneider (1834–1900), a dealer in natural history objects and corresponding member of the Goerlitz Society, Basle, Switzerland. Böttcher, a renowned bird collector, donated more than 100 birds to the Görlitz museum in 1861; the macaw might have been included in that gift (C. Düeker pers. comm.).

Naturhistoriska Riksmuseet, Stockholm (NRM) Two: NRM 569592. No date, locality or collector. Mount. Very old specimen from private collection of A. U. Grill (1752–92). Grill's collection was donated to NRM in 1829. No date when acquired by Grill, but probably *c*.1791–92 (U. Johansson pers. comm.). Locality given as 'Stockholm?', which U. Johansson (pers. comm.) interprets as it having been a cagebird in Stockholm. NRM 523094. No date, locality or collector. Mount. Purchased 1858 from G. A. Frank, a dealer in natural history objects in Amsterdam. Frank bought 80 birds from T. G. van Lidth de Jeude (1788–1863) and U. Johansson (pers. comm.) believes the NRM macaw came via this route, although it is unclear whether there is any documentation in favour of this supposition. The van Lidth de Jeude collection originated in the early 18th century and was assumed to include many old specimens (Boeseman 1970). U. Johansson (pers. comm.), however, notes that if a bird died in Amsterdam Zoo in that period, the NRM specimen may originate from there (see Lönnberg 1928). Moreno (1992) noted that a Cuban Macaw died in the Amsterdam Zoo in 1858, and presumed it was the NRM specimen.

Staatliches Museum für Tierkunde, Dresden (SMTD) One: SMTD 3466. No date, locality or collector. Mount. Moreno (1992) said it was part of an old collection from mid-19th century. Formerly a captive, by its frayed plumage (M. Päckert pers. comm.).

Eichsfelder Heimatmuseum, Heilbad Heiligenstadt (EHM) One: EHM IA1/310. No date, locality or collector (*fide* V. Merten). Mount. From among 750 bird and other natural history specimens accumulated by K. W. J. Strecker (1818–87) of Dingelstädt. Strecker donated, via his will, his collection to EHM in 1885.

Nationaal Natuurhistorisch Museum, Leiden (RMNH) One: RMNH.Aves.110095. No date or collector. Locality given as 'Cuba'. Mount. No further specimen or acquisition information (S. van der Mije pers. comm.).

Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ) One: MCZ 72526. No date, locality or collector. Original label missing. Ex-mount. From Lafresnaye Collection. Fine condition, but one wing clipped, suggesting a cagebird.

American Museum of Natural History, New York (AMNH) One: AMNH 205178. No date, locality or collector. Mount. Lacks tail. Died Berlin Zoo, date unknown. T. Barbour presented it to AMNH in 1923. Original label inscribed 'Psittacus tricolor Bechst. 1881 West Indies, 10189,' as well as a note in ink: 'Zool. Garden, Berlin.' Also: AMNH FARB 6199 ?Ara tricolor, proximal end of carpometacarpus Pleistocene, Baños de Ciego Montero; coll. B. Brown, 1918.

United States National Museum of Natural History, Smithsonian Institution, Washington DC (USNM) Two: USNM 135137. No date or locality; coll. Gundlach. Skin. Acquired by AMNH from Gundlach 13 December 1894. USNM 17167. No date, locality or collector. Mount. On exhibit in Hall 13 'Birds of the World.' History of this specimen involved and partially unsolved. Probably collected in Ciénaga de Zapata by Gundlach and carried with him, along with other birds, to Puerto Rico during Cuba's Ten Years War (1868–78). Barbour (1923) said Gundlach used the specimens, which also included two Ivory-billed Woodpeckers, to repay favours afforded by his friends, probably the apothecary and naturalist Tomás Blanco y González (1840–92) and naturalist Agustin Stahl (1842–1917).

With the encouragement of Blanco and Stahl, in 1866 the Padres Jesuitas de Puerto Rico invited Gundlach to build a natural history collection for the Colegio Seminario they had established in San Juan in 1865. Gundlach eventually made two extended trips to Puerto Rico to collect specimens for the Instituto Civil de Segunda Enseñanza de San Juan, established the same year as his first expedition (1873; López Yustos 1991). Stahl became a professor of natural history there, and Gundlach apparently provided the woodpecker and macaw specimens. Stahl and Blanco maintained the specimens at the Instituto, along with others collected by Gundlach during his 17 months in Puerto Rico. But, after the Spanish-American War (1898) and the Treaty of Paris, the Instituto was closed in 1899. Blanco had died in 1892 and Stahl was deported from Puerto Rico by the Spanish government in 1898, so the Instituto collection had lost its main advocates. Barbour (1923) thought Gundlach's Ivory-billed Woodpeckers were later acquired by AMNH, which matches at least one of the three specimens, AMNH 144873, a male, which has two labels, one of which reads, 'This bird was collected by Gundlach in Cuba and sold by him to Porto Rico High School.' The second label says 'Purchased from High School collection at St. Juan Porto Rico in 1901.' The AMNH catalogue adds 'collected in Cuba and sold to the Porto Rico High School where it was found' (P. Sweet in litt. 2012).

The macaw was apparently found in the Instituto by Major W. A. Glassford, US Army, Chief Signal Officer, stationed in San Juan, Puerto Rico during the post-Spanish-American War occupation by the US military. C. W. Richmond (1868–1932), who was in Puerto Rico collecting birds and herptiles with L. H. Stejneger (1851–1943) from 12 February to 19 April 1900, received the specimen from Glassford, whereupon Richmond deposited the macaw at USNM (accession date 16 May 1900).

Hypothetical or lost specimens.—Several rumours exist of additional specimens of Cuban Macaw in collections within Cuba, and some may have been extant quite recently. One rumour involves a macaw among the natural history exhibits at the Escuela 'Rafael María Mendive' (= Colegio Dolores or Convento de Dolores) at Santiago de Cuba. G. G. Hechavarría and L. O. Melián Hernández (pers. comm.) recalled that the exhibits contained a large collection of mounted birds including two Ivory-billed Woodpeckers and a Cuban Macaw. By the time JWW was permitted to visit the school in May 2006, all that remained were four badly damaged mounts, none of them a macaw. The school's director informed JWW that all of the other specimens had been destroyed during building reconstruction over the previous two years. The director said that, until the reconstruction, the natural history materials, including a macaw, had been well conserved and the most valuable specimens were in a case away from the main school activities.

That such specimens may have existed in the Escuela 'Rafael María Mendive' is supported by Leyva (1922), who noted a specimen of Ivory-billed Woodpecker and collection of butterflies made by Gundlach in the Museo Municipal de Santiago de Cuba, part of which may have found its way to the Escuela. O. H. Garrido (pers. comm.) recalled that he and F. García Montaña obtained a mounted specimen of the near-extinct Cuban Kite *Chondrohierax uncinatus wilsoni* from the same collection. Further, documents in the Archivo Nacional de Cuba include records that establish the collection of birds in the Escuela came from the Brooks family, which may link that collection to Gundlach. In 1884–85, Gundlach was guest of his friend Theodoro Brooks at Cafetal 'Jaguey' in the mountains of Yateras and, as characteristic of Gundlach, he may have given Brooks bird and other specimens to repay the family for their hospitality.

Barbour (1945) recounted that other macaw specimens had been in Cuban collections, including one in the cabinet of the Habana Academy of Sciences, but that disappeared and was rumoured to have gone to a notorious private collector abroad. Fuller (2001:

236) suggested that collector was Walter Rothschild. Barbour (1945) reported that another specimen was said to have been in a museum at Cárdenas, but thought it had been destroyed by insects; JWW found no record of it at Museo 'Oscar María de Rojas,' the museum presently holding natural history specimens in Cárdenas. Barbour (1945) claimed that yet another specimen was formerly in the Matanzas Institute.

Among Cuban Macaw specimens not currently accounted for in museum collections is one that was part of the collection of Prince Masséna d'Essling, Duke of Rivoli (1799–1863) (Souancé 1856: 57). Masséna accumulated a collection of 12,500 avian specimens, which he sold to Dr T. B. Wilson in 1846. Wilson gave the collection to the Academy of Natural Sciences of Philadelphia, but that collection does not contain a Cuban Macaw.

Discussion and Conclusions

Additional sources of information on West Indian macaws.—It is reasonable to hope that further paleontological and archaeological investigations will yield data to clarify the numbers of species and their distribution in the West Indies. Current work by W. Suárez & S. L. Olson in Cuba and their planned investigations of fossil and subfossil materials in Hispaniola may provide the type of information that will enable a better understanding of macaw populations. Investigation of Amerindian sites also may produce further information on macaw distribution and the interactions of native peoples with indigenous and introduced macaws.

Additional research of published and manuscript accounts by early travelers to the Antilles could yield confirmation of known reports of macaws. Also, correspondence archived in natural history museums may provide records of additional macaw specimens, now lost. We also hope that further surveys of museums, large and small, may reveal additional macaw specimens.

Another potential source of valuable information on West Indian macaws may lie in art museums, especially in Europe. Many parrot owners included macaws within formal portraits that hang on gallery walls. Macaws were considered prestige symbols, especially in the Renaissance, and often appear in the background or alongside their owners. Although often stylised, some depictions approximate species suggested for the West Indies. As Cooper & Armitage (2013) have suggested, examination of such art could prove a fertile field for learning more of macaw distribution and description. Greenway (1967) noted that a macaw in an early 17th century painting by Roeland Savery matches descriptions of some West Indian macaws. Macaws feature prominently in other paintings, including Bartholomeus van Bassen's (1590–1652) 'Renaissance interior with banqueters'. Hume & Walters (2012), however, urged caution in intrepreting such evidence as found in paintings, noting that artistic license may alter an artist's rendition of a bird, as well as the fact that the painting may have been made from fading memory, plagiarised or modified to suit composition.

Extinction of West Indian macaws.—Any one of the many problems that faced the Cuban and other West Indian macaws could have caused their extinctions, but the combination of environmental changes and human-related pressures most certainly sealed the fate of all Antillean macaws. Killing of adult macaws for subsistence or to protect crops probably had a substantial effect; although such persecution had been underway for some two millennia, the arrival of Europeans with their advanced guns must have vastly increased the efficiency with which macaws could be killed, thereby accelerating population declines. Similarly, harvest and trapping of wild macaws had its origin in Amerindian culture, but it was not until the opening of many markets, far and wide, that populations suffered to the point of extirpation. As Europeans colonised the Antilles, they increased the

speed and extent of habitat modification, through improved tools and ever-growing human populations. Particularly devastating was the practice of felling macaw nest trees to obtain young birds for personal use or trade. With the high demand for macaws, domestically and abroad, the harvest of nestlings and associated destruction of nesting habitat must have had a profound effect. The effects of other factors, including hurricanes and disease, are less easily predicted, but nonetheless potentially contributed to declines and extinctions. Disease, perhaps introduced via domestic poultry or exotic parrots bought to islands in trade, and to fill the demand for pets as local species became rare or disappeared, could have had an immediate, fateful effect on populations reduced to small numbers and restricted to remnant habitat. Island populations of birds are particularly susceptible to introduced diseases, often against which no defences exist. Whereas hurricanes have always been powerful forces of change in the West Indies, even the strongest storm probably had little effect on healthy populations of macaws when original habitats were extensive. Once habitat was fragmented by human activities and macaws had been reduced and confined to a few remnant habitats, a direct hit by a powerful storm would have destroyed forest critical to a population's survival, as well as perhaps killing birds outright. No matter whether one or a combination of factors led to the extinction of the Antillean macaws, certainly birds so rare, so easy to kill, so much in demand, and so very beautiful had little hope for survival.

Number of species and distribution in the Antilles.—Macaws certainly occurred over a wide area of the Caribbean, and on several islands, but the number of species is controversial. At this point, with available evidence, just how many species and on which islands depends in large part on how much credence is given to the vague accounts of early explorers, travelers and colonists. If all records unsupported by skins, fossil or subfossil

TABLE 3

Records of extinct *Ara* and *Auodorhyuchus* in the West Indies, with level of confidence of their former existence based on source of evidence.

Island	Species	Evidence	Confidence
Cuba	Ara tricolor	19 skins; fossil materials; last recorded 1850s	Specimens
Isla de Pinos	Ara tricolor	Multiple accounts; last recorded in 1864	Good, based on competent reporter
Jamaica	Ara erythruta	Multiple accounts; possible introduced species	Poor
	Ara erythrocephala	Multiple accounts; possible introduced species	Poor
	Ara gossei [Ara tricolor?]	Multiple accounts; possible introduced species	Good, based on competent observers
Hispaniola	Ara tricolor? or Ara unknown species	Multiple accounts	Poor
Puerto Rico	Ara autochthones	Skeletal material from kitchen midden	Specimen
St. Croix	Ara autoclithoues	Skeletal material from kitchen midden	Specimen
Montserrat	Ara undescribed sp.	Skeletal material from archaeological site	Specimen
Guadeloupe	Ara guadeloupensis	Multiple accounts & possible illustration	Moderate
Î	Auodorhyuchus purpurasceus	Multiple accounts; possible introduced species	Poor
Marie Galante	Ara cf. guadeloupeusis	Skeletal material from archaeological site; = Amazona imperialis?	Specimen
Dominica	Ara atwoodi	Single account	Poor
Martinique	Ara martinica	Single account; possible introduced species	Poor
	Anodorhynchus martinicus	Synonym of Ara martinica	-

remains are rejected, the number of species may be just three (Cuban Macaw, St. Croix Macaw, Montserrat Macaw) from five islands (Cuba, Isla de Pinos, Puerto Rico, St. Croix and Montserrat) (Table 3). Even among those species and islands with specimens, questions persist as to whether at least some species were native or transported there. If the list of probable species is extended to accept the most reasonable of those species supported only by written accounts, the number of islands and species is increased by only one: Gosse's Macaw from Jamaica. Yet even that species, the best described of all of the other purported macaws in the region, could have been based on a feral population of Scarlet Macaw introduced via trading and pet-keeping activities in the colonial period.

Among other suggested species, we consider the possibility of Guadeloupe Macaw moderately plausible. But, again, existence of Guadeloupe Macaw as endemic is confounded by possible introduced or transported species.

We consider all other species of macaws noted by early writers and formalised by Rothschild and others as poorly supported by current evidence. To date, no reliable verification is available of a macaw on Hispaniola. The existence of Dominica Macaw rests solely on Atwood's account, and macaws on that island may have their origin as an introduced or transported species. One named species, *Anodorhynchus martinicus*, is a synonym of *Ara martinicus*. Guadeloupe Violet Macaw was fairly well described as unique by early explorers, but there is a reasonable likelihood that this was a South American species transported to the island by Amerindians or colonists. Similarly, two, and perhaps all, of the three macaws listed by some for Jamaica were possibly feral birds resulting from releases or escapes of imported birds. Certainly, a vigorous trade in exotic parrots was established at the time accounts of macaws on Jamaica were recorded and their descriptions could relate to species known to have been traded on the island.

What we know of psittacid speciation and distribution in the Antilles supports the possibility, and even probability, of multiple endemic species of macaws, so there is no reason why each of the macaws described by explorer-naturalists could not have existed. Nevertheless, although the early accounts are alluring, without further proof, we recommend a conservative stance. We hope that future information, perhaps best searched for in the fossil and subfossil record, will provide solid proof that the primordial forests of most Antilles were alive with the squawks and brilliant plumages of macaws.

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